Biological Journal of the Linnean Society, 2020, **130**, 310–319. With 3 figures.

Trade-offs between burrowing and biting force in fossorial scincid lizards?

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Received 27 December 2019; revised 17 February 2020; accepted for publication 19 February 2020

Trade-offs are thought to be important in constraining evolutionary divergence as they may limit phenotypic diversification. The cranial system plays a vital role in many functions including defensive, territorial, predatory and feeding behaviours in addition to housing the brain and sensory systems. Consequently, the morphology of the cranial system is affected by a combination of selective pressures that may induce functional trade-offs. Limbless, head-first burrowers are thought to be constrained in their cranial morphology as narrow heads may provide a functional advantage for burrowing. However, having a wide and large head is likely beneficial in terms of bite performance. We used 15 skink species to test for the existence of trade-offs between maximal push and bite forces, and explored the patterns of covariation between external head and body morphology and performance. Our data show that there is no evidence of a trade-off between bite and burrowing in terms of maximal force. Species that generate high push forces also generate high bite forces. Our data also show that overall head size covaries with both performance traits. However, future studies exploring trade-offs between force and speed or the energetic cost of burrowing may reveal other trade-offs.

ADDITIONAL KEYWORDS: covariation – cranial system – divergence – head-first burrowers – morphology – skink.

INTRODUCTION

The phenotype of an organism reflects the selective pressures exerted by activities that are essential to its survival and its reproduction (Arnold, 1993). Sometimes, however, the functional demands exerted by different performance traits may result in trade-offs. Indeed, functional trade-offs arise when different functions exert conflicting pressures on the same anatomical structures (Arnold, 1992; Van Damme *et al.*, 2002, 2003). Previous studies have further suggested that trade-offs may in some cases limit phenotypic variation by constraining evolutionary divergence (Vanhooydonck *et al.*, 2001; Levinton & Allen, 2005; Konuma & Chiba, 2007; Herrel *et al.*, 2009). The cranial system plays a vital role in many activities including defensive, territorial, predatory and feeding behaviours in addition to housing and protecting the brain and major sensory organs (Andrews *et al.*, 1987; Cooper & Vitt, 1993; Herrel *et al.*, 2007; Kohlsdorf

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et al., 2008; Dumont *et al*., 2016). Consequently, the morphology of the cranial system is affected by these combined selective pressures which may potentially induce functional trade-offs.

The hypothetical trade-off between biting and borrowing performance is particularly interesting in limbless burrowing animals. These organisms are obligate head-first burrowers and the evolution of their morphology is thought to be constrained. Indeed, because the energy required for burrowing increases exponentially with body and head diameter (Navas *et al*., 2004), having a thin body and a narrow head may provide a functional advantage for burrowing. Yet, this is likely detrimental in terms of bite performance (Verwaijen *et al*., 2002; Navas *et al*., 2004; Herrel & O'Reilly, 2006; Vanhooydonck *et al*., 2011; Baeckens *et al*., 2017; Hohl *et al*., 2017). Maximum bite force has been suggested to limit the type and size of food an animal can eat (Herrel *et al*., 1999, 2001, 2008; Aguirre *et al*., 2003; McBrayer & Corbin, 2007; Edwards *et al*., 2013). Consequently, a cranial form optimized for soil penetration may compromise the types of food an animal can eat and *vice versa* (Andrews *et al*., 1987; Barros *et al*., 2011; Baeckens *et al*., 2017).

Burrowing is a complex behaviour that remains rather poorly understood in limbless head-first burrowing vertebrates (but see for example Gaymer (1971); Gans (1973); O'Reilly *et al*. (1997); Teodecki *et al*. (1998); Navas *et al*. (2004); De Schepper *et al*. (2005)). The maximal push force that an animal can generate is likely important as it may allow an animal to penetrate a greater variety of soil types, and thus expand its resource base in terms of potential habitat and food resources. As limbless species burrow by recruiting muscles along the long axis of the body (Rieppel, 1981; Navas *et al*., 2004; Vanhooydonck *et al*., 2011; Hohl *et al*., 2017), the diameter and size of the body should be related to the maximal push force it can generate. However, to facilitate soil penetration the width of the head should rather be narrow as this optimizes the pressure for a given force (e.g. Measey & Herrel, 2006; Herrel & Measey, 2010; Barros *et al*., 2011). Moreover, the speed by which it can penetrate the soil (and not only the force generated) is also likely a factor significantly contributing to the burrowing performance (Ducey *et al*., 1993; Teodecki *et al*., 1998; Vanhooydonck *et al*., 2011). Although few quantitative data exist, a previous study suggested the presence of a trade-off between bite force and burrowing speed in a limbless skink, *Acontias percevali,* mediated by the conflicting demands on head dimensions (Vanhooydonck *et al*., 2011). However, whether this is more generally the case and whether trade-offs also exist between bite force and push force remains unknown. As burrowing force is dependent on the axial musculature, different anatomical traits are responsible for the generation of bite force vs. burrowing force. Consequently, trade-offs between these two performance traits, if present, are not mediated by direct functional conflict for the optimization of single functional trait. Rather, burrowers can be expected to have narrow heads for efficient soil penetration which may come at a cost of bite force.

Here, we test for the presence of a trade-off between maximal bite force and the maximal push force in a range of burrowing and leaf-litter dwelling skinks. Scincid lizards represent an ideal study system as this family includes a variety of ecologies and morphologies with quadrupedal surface-dwelling species, epigeal serpentiform species with partially reduced front- and/or hindlimbs, burrowing completely limbless species, and a plethora of intermediate forms (Pianka & Vitt, 2003; Miralles *et al*., 2015; Wagner *et al*., 2018; Bergmann & Morinaga, 2019). At least 15 independent evolutions of a serpentiform body form have taken place within the group (Benesh & Withers, 2002; Miralles *et al*., 2012) allowing for a robust framework to test for associations between life-style, performance and morphology. Consequently, we also explore the patterns of covariation between head and body morphology and the two performance traits studied here (bite force and push force).

MATERIALS AND METHODS

Animals

Morphological measurements were performed on 180 individuals and performance measurements were obtained for 171 individuals for bite forces and 159 for push forces across 14 different species (Table 1). Animals were sampled between 2000 and 2017. The specimens were adults of often unknown sex. Data were collected *in situ* in the field or in the lab for species that were obtained through the pet trade. An additional five individuals of the species *Pygomeles braconnieri* from the collections of the National Museum of Natural History in Paris were used for morphological measurements.

Morphometrics

Each individual was weighed using an electronic balance (Ohaus, ± 0.1 g). Head length, head width, head depth and lower jaw length were measured using a digital caliper (Mitutoyo, ± 0.01 mm) as described previously (Herrel and Holanova, 2008). The snout-vent length was measured by stretching the animals along a ruler (± 1 mm).

Maximal push force

Maximal push forces were measured in the field or in the lab following the protocol described in Vanhooydonck

Table 1. Mean and standard deviation of morphological and functional data for the 14 species included in this study

Species	SVL (mm)	Head length (mm)	Head width (mm)	Head depth (mm)	Lower jaw length (mm)	Mass (g)	Body diameter (mm)	Push force (N)	Bite force (N)
Acontias kgalagadi	116.12 ± 12.10 (N = 5)	7.27 ± 0.49 (N = 5)	3.60 ± 0.20 (N = 5)	3.23 ± 0.86 (N = 5)	5.70 ± 0.34 (N = 5)	1.95 ± 0.64 (N = 5)	4.28 ± 0.37 (N = 5)	0.56 ± 0.20 (N = 5)	1.16 ± 0.40 (N = 5)
Acontias litoralis	108.34 ± 16.64 (N = 47)	5.95 ± 0.91 (N = 47)	3.01 ± 0.29 (N = 47)	2.54 ± 0.26 (N = 47)	5.09 ± 0.76 (N = 47)	1.39 ± 0.45 (N = 47)	3.38 ± 0.48 (N = 47)	0.51 ± 0.25 (N = 41)	0.73 ± 0.19 (N = 42)
Acontias meleagris	194.24 ± 16.34 (N = 6)	10.43 ± 1.08 (N = 6)	5.81 ± 0.90 (N = 6)	4.56 ± 0.55 (N = 6)	7.67 ± 1.16 (N = 6)	9.74 ± 2.85 (N = 6)	7.26 ± 1.30 (N = 6)	3.13 ± 0.47 (N = 3)	8.99 ± 1.77 (N = 6)
Acontias percivali	246.83 ± 12.48 (N = 12)	13.88 ± 1.34 (N = 12)	8.00 ± 0.75 (N = 12)	6.98 ± 0.70 (N = 12)	13.25 ± 0.76 (N = 7)	16.87 ± 5.07 (N = 12)	9.28 ± 0.99 (N = 12)	5.32 ± 0.85 (N = 12)	10.08 ± 3.06 (N = 12)
Chalcides ocellatus	80.88 ± 24.41 (N = 16)	11.85 ± 2.76 (N = 16)	7.76 ± 2.18 (N = 16)	6.53 ± 1.95 (N = 16)	12.96 ± 3.04 (N = 16)	10.28 ± 6.88 (N = 16)	10.77 ± 3.26 (N = 16)	4.56 ± 1.39 (N = 14)	6.82 ± 4.19 (N = 13)
Chalcides sepsoides	83.41 ± 5.73 (N = 17)	9.90 ± 0.48 (N = 17)	5.93 ± 0.33 (N = 17)	5.05 ± 0.24 (N = 17)	9.97 ± 0.71 (N = 17)	4.66 ± 1.02 (N = 17)	7.45 ± 0.65 (N = 17)	2.46 ± 0.75 (N = 17)	4.12 ± 0.75 (N = 17)
Mochlus sundevallii	83.64 ± 18.88 (N = 10)	12.40 ± 2.40 (N = 10)	7.68 ± 1.55 (N = 10)	6.20 ± 1.19 (N = 10)	12.64 ± 2.29 (N = 10)	9.83 ± 6.55 (N = 10)	6.97 ± 1.32 (N = 7)	1.56 ± 1.25 (N = 7)	12.33 ± 6.45 (N = 10)
Pygomeles braconnieri	109.67 ± 37.11 (N = 6)	10.61 ± 1.72 (N = 6)	6.25 ± 1.44 (N = 6)	5.06 ± 0.99 (N = 6)	9.40 ± 1.98 (N = 6)	12.78 ± 7.34 (N = 6)	7.99 ± 3.85 (N = 6)	7.50 (N = 1)	9.36 (N = 1)
Scelotes bipes	74.56 ± 10.67 (N = 12)	6.18 ± 0.57 (N = 12)	3.22 ± 0.58 (N = 12)	2.62 ± 0.42 (N = 12)	5.46 ± 0.58 (N = 12)	1.56 ± 0.73 (N = 11)	3.84 ± 0.66 (N = 12)	0.36 ± 0.16 (N = 8)	1.33 ± 0.70 (N = 11)
Scelotes montispectus	61.58 (N = 1)	6.81 (N = 1)	3.32 (N = 1)	2.83 (N = 1)	6.40 (N = 1)	1.00 (N = 1)	3.55 (N = 1)	0.55 (N = 1)	1.27 (N = 1)
Scincus scincus	92.20 ± 3.04 (N = 5)	18.76 ± 0.72 (N = 5)	10.65 ± 0.75 (N = 5)	9.92 ± 0.88 (N = 5)	18.44 ± 1.47 (N = 5)	18.75 ± 3.96 (N = 5)	14.76 ± 1.35 (N = 5)	7.72 ± 2.04 (N = 5)	18.39 ± 3.59 (N = 5)
Typhlosaurus caecus	171.30 ± 34.42 (N = 32)	6.70 ± 0.80 (N = 32)	3.39 ± 0.54 (N = 32)	1.98 ± 0.27 (N = 32)	4.67 ± 0.77 (N = 32)	3.42 ± 1.48 (N = 32)	4.27 ± 0.72 (N = 32)	2.11 ± 1.02 (N = 32)	3.01 ± 1.60 (N = 32)
Typhlosaurus lomiae	106.33 ± 10.49 (N = 9)	5.52 ± 0.29 (N = 9)	2.60 ± 0.09 (N = 9)	2.13 ± 0.07 (N = 9)	3.99 ± 0.50 (N = 9)	0.92 ± 0.19 (N = 9)	2.91 ± 0.17 (N = 9)	0.32 ± 0.08 (N = 8)	0.45 ± 0.12 (N = 9)
Typhlosaurus vermis	195.33 ± 48.57 (N = 6)	6.76 ± 0.99 (N = 6)	3.18 ± 0.37 (N = 6)	2.67 ± 0.33 (N = 6)	5.40 ± 0.86 (N = 6)	2.68 ± 1.09 (N = 6)	3.56 ± 0.39 (N = 6)	1.58 ± 0.33 (N = 5)	0.93 ± 0.25 (N = 6)

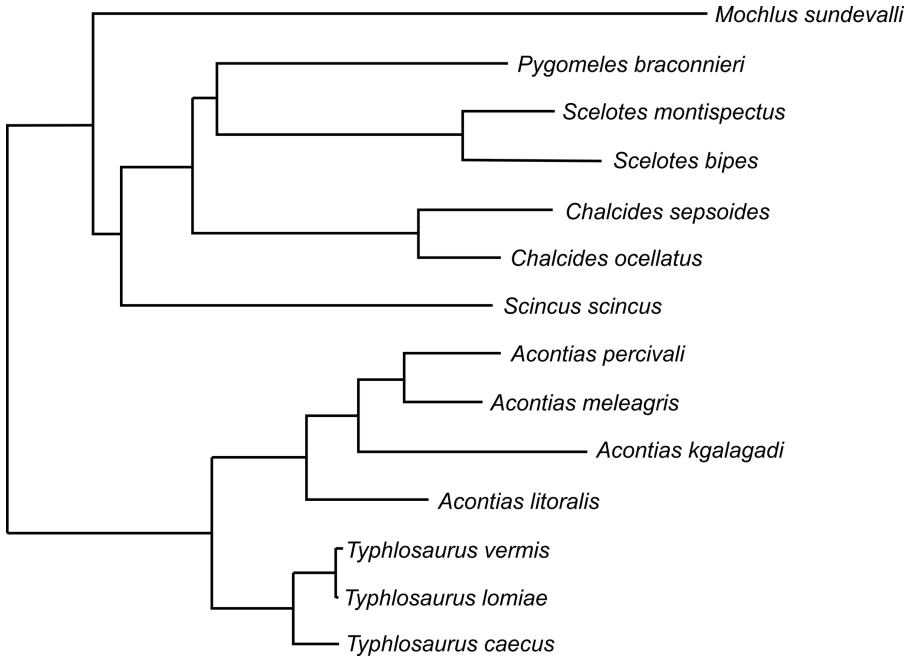

Figure 1. Phylogeny used in the analyses modified from Pyron et al. (2013).

et al. (2011). Measurements of peak push forces during burrowing were made using a custom piezoelectric force platform (Kistler Squirrel force plate, ± 0.1 N, Kistler Inc., Switzerland). The force platform was positioned on a custom-designed metal base and connected to a charge amplifier (Kistler Charge Amplifier type 9865, Kistler Inc.). A Perspex block with 1 cm-deep holes of different diameters was mounted on the force plate, level with the front edge. One of the holes was loosely filled with soil from the container of the animal that was tested. A Perspex tunnel with a diameter similar to the maximal body diameter of the test animal was mounted on the metal base in front of (but not touching) the force plate, and aligned with the soil-filled hole in the Perspex block. First, a skink was introduced into the tunnel and allowed to move through it until reaching the soil-filled chamber. Next, the animal was stimulated to burrow into the soil by tapping the end of the tail sticking out of the tunnel, or by prodding the animal inside the tunnel with the blunt end of a thin wooden stick. Forces were recorded during a 60 s recording session at 500 Hz, and three trials were performed for each individual, with at least 1 h between trials. Forces were recorded in three dimensions using the Bioware software (Kistler Inc.). For each individual we then extracted the highest peak resultant force across all trials as an indicator of that animal's maximal push force.

Maximal bite force

Maximal bite forces were measured in the field or the lab following Herrel *et al*. (1999). In brief, *in vivo* bite forces were measured using an isometric Kistler force transducer (type 9203, Kistler Inc.) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5058 A, Kistler Inc.). Biting causes the upper plate to pivot around the fulcrum, and thus pull is exerted on the transducer. Capture of the animals typically resulted in a characteristic threat response where the jaws are opened maximally. The free end of the holder was then placed between the jaws of the animal, which immediately resulted in fierce and prolonged biting. The gape angle (± 30 °) and the place of application of the bite force was standardized with animals always biting at the tips of the jaws. Measurements were repeated five times for each animal and the maximum value recorded was considered to be the maximal bite force for that animal.

Analyses

Morphometric and force data were Log_{10}-transformed before analysis to ensure normality and homoscedasticity.

All analyses were performed in R (v.3.4.0) while taking into account the phylogenetic relationships among species. The phylogenetic framework

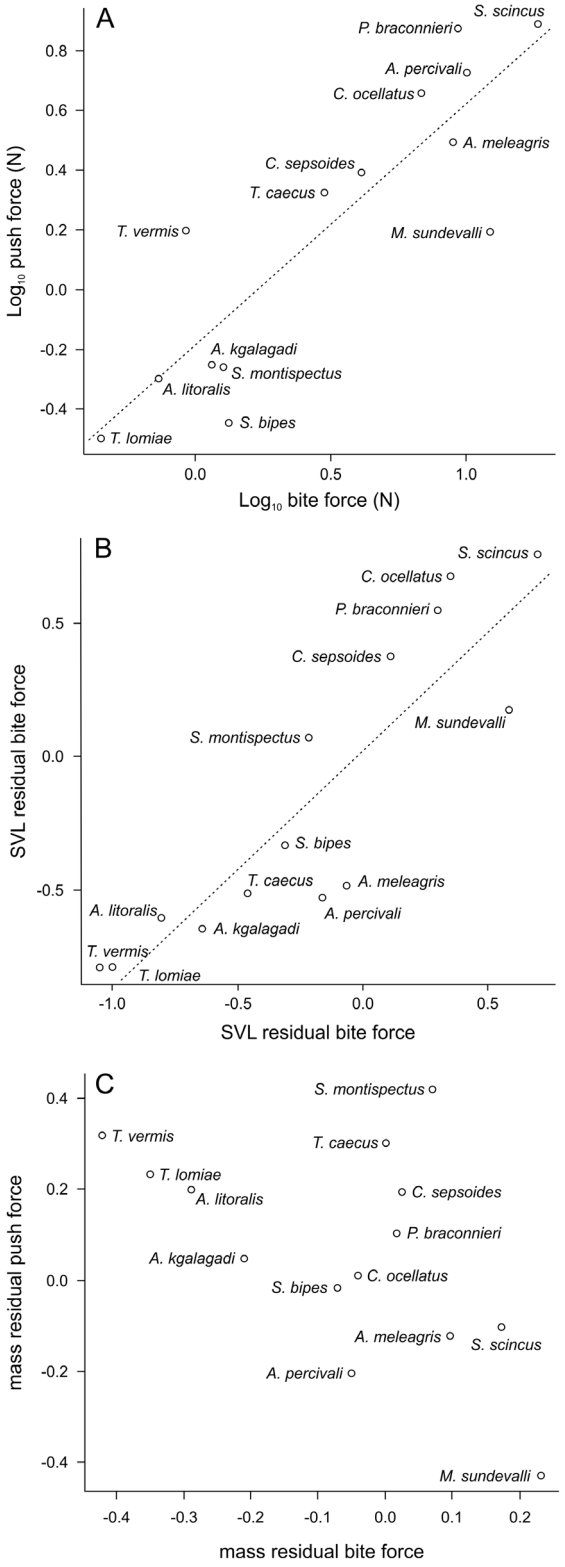

Figure 2. Phylogenetic regressions of species averages of maximal bite force against maximal push force. (A) Absolute push force is significantly correlated with absolute bite force. (B) Residual bite force is significantly and positively correlated with residual push force when correcting for overall snout-vent length. (C) Residual bite force is no longer related to variation in residual push force when corrected for variation in body mass.

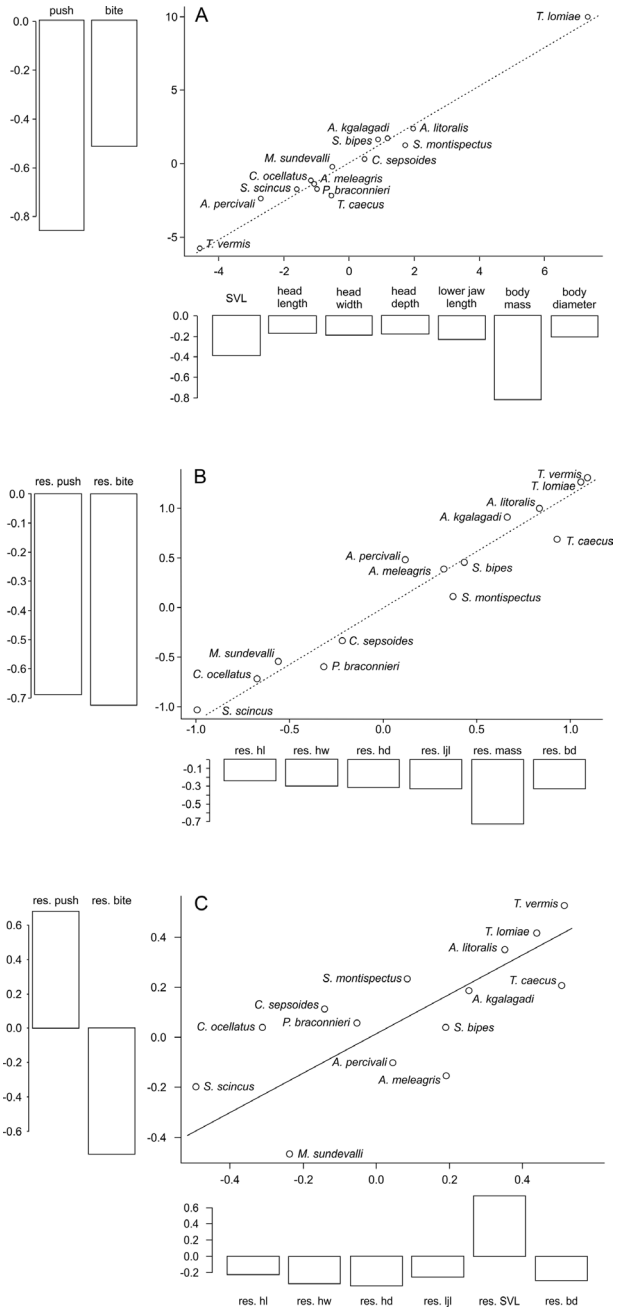

Figure 3. Covariance between morphological and performance data. (A) Phylogenetic two-block partial least square analysis between morphology and performance illustrating that more robust species (i.e. with greater body mass and bigger heads) produce greater push and bite forces. (B) Two-block partial least square analysis on the force and morphological data corrected for variation in snout-vent length. Species with relatively higher mass, heads size and body diameter produce greater bite and push forces. (C) Two-block partial least square analysis on the force and morphological data corrected for variation in body mass showing that species that are relatively more elongate (higher snout-vent length for their mass) show relatively higher push forces. In contrast, species that are stockier, less elongate and with bigger heads produce relatively higher bite forces.

used was obtained from the molecular data set of Pyron *et al.* (2013); Fig. 1. This required the reconstruction of a phylogeny by pruning the tree to include only species for which we had performance and morphological data. First, a phylogenetic generalized least squares (PGLS) regression was

run in R (function gls with corBrownian in Phytools (Revell, 2012)) with the mean maximal push force per species against mean maximal bite forces to test for the presence of a trade-off between bite and push force. To test for co-variation between morphology and performance we ran a phylogenetic two-block partial least squares analysis (φ2bPLS) using the function 'phylo.integration' implemented in 'geomorph' in R (Adams *et al*., 2013). This method quantifies the degree of association between two data matrices. It is a descriptive multivariate analysis robust to multicollinearity between variables and therefore suitable for the use of morphometric and performance variables. The analysis generates axes that explain the covariance between the two data matrices.

As body size simultaneously impacts head and body dimensions and forces, we ran PGLS analyses with snout-vent length (SVL) or body mass as our predictor and morphometric and performance traits as our independent variables and extracted the unstandardized residuals. Next, we used a Pearson correlation test to explore the existence of a trade-off between our two residual performance traits independent of variation in overall body size. Finally, we ran a two-block partial least squares analyses (2BPLS) on the residual data to explore patterns of covariation between morphology and performance independent of variation in overall size using 'two.b.pls' script of the 'geomorph' package (Adams *et al*., 2013), and 'pls2B' script of the 'Morpho' package (Schlager, 2013) in R.

RESULTS

Trade-offs between bite force and push force

The linear regression taking into account phylogeny shows that maximum push force is positively correlated with maximal bite force (PGLS: r = 1.36, P < 0.001), suggesting that species that produce strong push forces are also those who produce strong bite forces (Fig. 2A). Analyses performed on the snout-vent length corrected data show a similar result (r = 0.89, P < 0.001) with animals that bite harder for a given size also being better pushers (Fig. 2B). However, when correcting force measurements for body mass, residual bite force was no longer correlated with residual push force (r = -0.63, P = 0.053; Fig. 2C). An inspection of the plot (Fig. 2C) suggests that more elongate and smaller species like *Typhlosaurus vermis* and *T. lomiae* as well as *Acontias litoralis* and *A. kgalagadi* tend to have relatively higher push forces whereas the stockier, larger species like *Scincus scincus*, *A. meleagris*, and *Mochlus sundevalli* appear to have relatively large bite forces but low push forces.

Covariation between morphology and performance

The phylogenetic 2BPLS analysis was significant (rPLS = 0.983, P = 0.001). Heavier, larger and wider animals with longer, taller and wider heads produce larger forces (Fig. 3A). The 2BPLS analysis run on the size-corrected data was also significant (rPLS = 0.969, P < 0.001; Fig. 3B). This analysis indicates that the maximal push force and the maximal bite force co-vary, both principally with overall head and body robustness, with animals that are more elongate producing relatively lower push and bite forces. An analysis on the size corrected data using body mass was also significant (rPLS = 0.73, P = 0.012), yet showed a different pattern. This analysis shows that more elongate animals produce relatively higher push forces whereas the more robust limbed species with wide heads and bodies produce low push but high bite forces for their body mass (Fig. 3C).

DISCUSSION

Our results, based on a broad range of burrowing and leaf-litter dwelling skinks, show that there is no direct trade-off between bite force and burrowing force in this group. Species that produce strong push forces are also those which produce strong bite forces in both absolute and relative terms. These results suggest that whereas bite force may trade-off with burrowing speed (Teodecki *et al*., 1998; Vanhooydonck *et al*., 2011) this may not be the case for push force. Indeed, the same traits that favour increased bite force (large, robust heads and wide bodies) also appear to favour high push forces, at least in absolute terms. This makes intuitive sense as the muscles used to generate both bite and push force are positioned to the lateral side of the body in scincid lizards (Huyghe *et al*., 2009; Vanhooydonck *et al*., 2011). For example, the external adductor muscle is one of the largest contributors to overall bite force generation and lies external to the mandible (Vanhooydonck *et al*., 2011). Similarly, the iliocostalis and longissimus muscles that generate the push forces measured are also positioned laterally to the vertebral column. Consequently, wider heads and wider bodies should induce an increase in both absolute bite and push force. However, whereas these traits may indeed favour absolute force, the speed by which animals can penetrate the soil may be negatively impacted by the presence of wider heads and bodies (Teodecki *et al*., 1998; Vanhooydonck *et al*.,

2011). Moreover, the energetic cost of burrowing may also be negatively impacted by these traits (Navas *et al*., 2004). However, whereas the limbed species are the best biters in absolute terms and when corrected for body mass the more elongate specialized burrowers (e.g. *Acontias*, *Scelotes*, *Typhlosaurus*) actually produce greater push forces. Indeed, the specialized head-first limbless burrowers like *Acontias* or *Typhlosaurus* have higher push forces for their mass despite being more elongate and less robust. Moreover, individuals of these species were usually captured at deeper soil depths and in less sandy soils (A. Herrel & J. Measey, pers. obs.) suggesting that they are overall better at burrowing. Thus, rather than absolute push force relative push force may be the principal driver of burrowing specialization. However, given the paucity of quantitative data on soil hardness and burrow depth in fossorial animals a quantitative analysis of these patterns is not possible. Additionally, it would be of interest to gather similar data on other groups of fossorial skinks from different radiations (Australia, Madagascar, the Philippines, see Wagner *et al*. (2018); Morinaga & Bergmann, 2020) as the data in the present study are strongly biased towards African skinks, especially the Acontinae.

Traits affecting bite and burrow performance

Despite the absence of trade-offs, we hypothesized that morphological traits that co-vary with each type of performance trait might be different. In contrast to our prediction, the phylogenetic 2BPLS analysis showed that all traits covaried with both forces, especially body mass. Heavier, larger and wider animals with long, tall and wide heads produced greater forces in absolute terms. However, analyses performed on the size corrected data showed different results. Indeed, whereas the relative mass and the diameter of the body and head relative to the length of the animal appear to drive both variation in bite force and push force, as with absolute data, when correcting for body mass this was no longer the case. More robust and less elongate limbed species with wide and deep heads like *Chalcides ocellatus, Scincus scincus* or *Mochlus sundevalli* produce relatively high bite, yet low push forces (see Fig. 3C). This is expected as it had been shown that the maximal bite force generated by an individual is determined by its head dimensions (Verwaijen *et al*., 2002; Navas *et al*., 2004; Herrel & O'Reilly, 2006; Vanhooydonck *et al*., 2011; Baeckens *et al*., 2017; Hohl *et al*., 2017). Maximum push force has, however, been suggested to be determined by the total length of the body (Rieppel, 1981; Navas *et al*., 2004; Measey & Herrel, 2006; Barros *et al*., 2011; Vanhooydonck *et al*., 2011; Hohl *et al*., 2017) as also suggested by our data. Indeed, more elongate species of the genera *Typhlosaurus* as well as the more elongate *Acontias* species (*A. litoralis, A. kgalagadi*) showed high push forces yet low bite forces (Fig. 3C). It would consequently be of interest to perform finer scale analyses of head shape or skull shape using geometric morphometric approaches. This may also allow teasing apart of differences between the back and the front of the skull likely impacted by constraints on biting vs. burrowing (Cornette *et al*., 2015).

In conclusion, we were unable to demonstrate a trade-off between bite and push force. Whereas both forces were positively correlated in both absolute and relative terms, the traits driving variation in force differed when body size was taken into account. For a given body mass the more elongate forms produced higher push forces, possibly due to the fact that to create push forces the axial muscles along the entire body are used. Ecological as well as detailed anatomical studies are clearly needed to better understand the relationships between morphology, performance and ecology as well as the anatomical drivers of variation in performance.

ACKNOWLEDGMENTS

We would like to thank Günter Wagner and an anonymous reviewer for helpful and constructive comments on a previous version of this manuscript and Anne-Claire Fabre for extensive help with the analyses and without whom this paper would not have been possible. South African fieldwork was conducted in under provincial research permits in the Western Cape (AAA007-00035-0035), Limpopo (333-00015) and Northern Cape (FAUNA 1243/2008). AH and JM thank Krystal Tolley and the National Research Foundation (NRF) of South Africa (South African Biosystematics Initiative-SABI, Key International Science Collaboration-KISC), and ethics clearance from SANBI (0010/08).

FUNDING This work was supported by a grant from Agence Nationale de la Recherche under the LabEx ANR-10-LABX-0003-BCDiv, in the program 'Investissements d'avenir' n\u0001 ANR-11-IDEX-0004-02.

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